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Prey switching behaviour in the planktonic copepod *Acartia tonsa*

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ABSTRACT: The copepod *Acartia tonsa* has 2 different prey encounter strategies. It can generate a feeding current to encounter and capture immobile prey (suspension feeding) or it can sink slowly and perceive motile prey by means of mechanoreceptors on the antennae (ambush feeding). We hypothesized that *A. tonsa* adopts the feeding mode that generates the highest energy intake rate; i.e. that prey selection changes according to the relative concentrations of alternative prey (prey switching) and that the copepods spend disproportionately more time in the feeding mode that provides the greatest reward. Based on earlier observations, we also hypothesized that turbulence changes food selection towards motile prey. We tested these hypotheses by examining feeding rates and behaviour in adult females of *A. tonsa* feeding in mixtures of 2 prey organisms, a diatom (*Thalassiosira weissflogii*) and a ciliate (*Strombidium sulcatum*). Our data demonstrate prey switching in *A. tonsa*, both in terms of behaviour and in terms of feeding rates on the alternative prey. The time allocated to ambush and suspension feeding changed with the composition of the food, and clearance of diatoms was, accordingly, negatively related to the availability of ciliates. In contrast, clearing of ciliates was almost constant and independent of the availability of the alternative prey (diatoms), probably because this particular ciliate species (in contrast to most other microzooplankters) is unable to escape a feeding current and, thus, can also be captured by suspension feeding copepods. Finally, we demonstrate that turbulence favours the selection of ciliates as prey. We suggest that prey switching by copepods may provide survival windows for microzooplankters during blooms of net phytoplankton because predation pressure from the copepods is then less. This may explain why microzooplankton populations often peak concurrently with net phytoplankton blooms and apparently independently of their own food.

KEY WORDS: Prey switching · Prey selection · Behaviour · Copepod · *Acartia tonsa*

INTRODUCTION

Planktonic copepods feed on a variety of items, and the relative rates at which copepods ingest these various types of food particles normally do not reflect their relative abundance in the environment (e.g. Vanderploeg 1994). Thus, copepods are selective feeders. This has implications both for the dietary well being of the copepods (Kleppel 1993) and for the structure of pelagic food webs (e.g. Landry 1981). There is a con-

siderable body of literature describing prey selection in copepods (e.g. Wiadnyana & Rassoulzadegan 1989), but few studies have examined the behavioural components of prey selection (e.g. Greene & Landry 1985, Vanderploeg et al. 1988).

Food selection may be either passive or active (Greene 1985). Passive selection is the result of differential prey vulnerability or perceptual biases of the predator, and prey selection in a mixed-prey assemblage can be predicted from single-prey experiments. Food-particle size spectra in planktonic copepods (e.g. Frost 1977, Bartram 1981, Vanderploeg et al. 1984, Berggreen et al. 1988) suggest that this type of selection occurs, although the exact mechanisms of particle size selection are not fully understood (Paffenhöfer &

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Lewis 1990). Active selection, on the other hand, implies a behavioural response with active dietary choice; for example, that the predator rejects or attempts the capture of an encountered prey particle, or the ingestion of a captured particle, on the basis of its chemical, physical or visual appearance. Active selection in this sense has been demonstrated for copepods (e.g. DeMott 1988, Vanderploeg 1994).

Another potential active food selection mechanism, different from individual particle acceptance/rejection, was suggested for the common coastal copepod *Acartia tonsa* by Saiz & Kiørboe (1995); the suggestion was based on behavioural observations reported by Jonsson & Tiselius (1990). *A. tonsa* exhibits 2 different modes of feeding behaviour. When presented with diatoms (or other immotile prey) the copepod generates a feeding current and captures diatoms that arrive with the feeding current (suspension feeding). When exposed to ciliates, and presumably to other motile prey, the copepod engages in ambush feeding. It does not produce a feeding current but sinks slowly through the water. Ciliates are sensed by mechanoreceptors on the antennae and, once the ciliate has been perceived, the copepod attempts to capture it. Saiz & Kiørboe (1995) hypothesized that each of the 2 feeding modes would be the more efficient for 1 of the 2 respective types of prey; most or many ciliates will be able to sense and escape a feeding current, while mechanoreception would not be useful for detecting diatoms. In this case, selection between the 2 types of prey would be the result of an active behavioural response.

Optimal foraging theory would predict that a predator adopts the feeding behaviour that generates the highest intake rate of energy (or another limiting substance). For *Acartia tonsa* this implies that prey selection changes with the relative concentrations of the alternative prey organisms and that the copepod spends disproportionately more time in the feeding mode that provides the greatest reward. Thus, we hypothesise that *A. tonsa* shows frequency-dependent prey selection—or prey switching—and we propose that the reason for this is a change in the allocation of time to different feeding behaviours.

For planktonic predators it is prey encounter rate rather than the prey abundance that determines the feeding conditions. Through modelling and single-prey experiments, Kiørboe & Saiz (1995) and Saiz & Kiørboe (1995) showed that moderate turbulence (dissipation rate of ca $2 \times 10^{-2} \text{ cm}^2 \text{ s}^{-3}$) enhances the prey encounter and, hence, feeding rate by a factor of ca 4 in *Acartia tonsa* in the ambush mode, while suspension feeding is not significantly affected. This is because encounters with prey depend upon the velocity difference between predator and prey and because the turbulent water motion is rapid relative to the sinking

velocity of the copepod (ambush mode) but slow relative to the feeding current velocity (suspension mode). This difference further implies that ciliates would come to dominate the diet at lower relative concentrations in turbulent compared to calm conditions.

The purpose of the present study was to examine experimentally prey selection and switching behaviour in *Acartia tonsa*. Our general hypothesis can be broken down into the following explicit hypotheses: (1) feeding on ciliates and feeding on diatoms are mutually exclusive; (2) *A. tonsa* switches from feeding preferentially on one prey species to the other as the relative concentrations of the 2 prey change; and (3) turbulence will change prey selection towards ciliates. To test these hypotheses we measured clearance and ingestion rates on diatoms and ciliates in mixtures with different concentrations of the 2 types of prey, both in calm and in turbulent water. These experiments were supplemented by behavioural observations conducted in calm water. Our study demonstrates that the feeding mode of *A. tonsa* changes with prey availability, that this causes prey switching, and that turbulence changes prey selection towards ciliates.

MATERIAL AND METHODS

The experiments were conducted with the diatom *Thalassiosira weissflogii* (equivalent spherical diameter, ESD, ca $13 \mu\text{m}$) and the ciliate *Strombidium sulcatum* (ESD $30 \mu\text{m}$) as prey, and adult females of the copepod *Acartia tonsa* as predator. The copepods were grown in a laboratory culture (Støttrup et al. 1986) at 16 to 18°C and only females that had matured within a week were used for the experiments. *T. weissflogii* were grown in batch cultures at a light intensity of ca $100 \mu\text{E m}^{-2} \text{ s}^{-1}$; only cells from exponentially growing cultures were used. The ciliates were grown on bacteria in a wheat-grain medium, in darkness, and at ca 18°C. One liter bottles were inoculated 2 to 4 d prior to use, and ciliates occurred at concentrations of ca 500 to 1000 ml^{-1} in the cultures when ready for use. All feeding experiments were conducted in darkness at $15 \pm 0.5^\circ\text{C}$.

Feeding experiments. Bottle experiments to measure feeding rates largely followed Saiz & Kiørboe (1995). Female copepods were acclimated for 24 h in filtered seawater at 15°C prior to experiments. Calm-water incubations were conducted in 1.1 l (functional response experiments) or 2.3 l screw-cap bottles (all other experiments) on a slowly rotating (0.2 rpm) wheel. Incubations in turbulence were conducted in 2.3 l cylindrical oscillating grid chambers as described by Saiz & Kiørboe (1995). The grid (70% open area) oscillated at 3 strokes min^{-1} , yielding a turbulent dissi-

pation rate of $2.3 \times 10^{-2} \text{ cm}^2 \text{ s}^{-3}$. This is close to the dissipation rate that yields the highest positive effect on clearance of ciliates (*Strombidium sulcatum*) by *Acartia tonsa* and can be considered representative of the turbulence generated in the upper mixed layer by moderately strong winds (Kjørboe & Saiz 1995). Experimental suspensions were prepared in $0.2 \mu\text{m}$ filtered seawater to which diatoms and ciliates were added in the desired amounts. EDTA ($10 \mu\text{M}$) and bacteria ($>10^6 \text{ ml}^{-1}$; from $5 \mu\text{m}$ filtrate of ciliate culture) were also added to ensure survival and growth of ciliates. Concentrations of ciliates and diatoms were measured at the start and end of each experiment: one liter samples were preserved with acid Lugol's solution (10 ml l^{-1}), and aliquots were filtered onto 2 and $5 \mu\text{m}$ membrane filters, and 300 to 400 cells of each were counted at $100\times$ magnification. For all experimental conditions we had 4 replicates and 4 controls (without copepods), except for the functional response experiment, in which there were only 3 replicates and 3 controls. All incubations lasted ca 20 h. Ingestion and clearance rates and average concentrations were calculated according to the equations of Frost (1972).

We first examined the effect of ciliates on the calm-water functional response of *Acartia tonsa*'s ingestion of diatoms to variations in the diatom concentration. In one experiment the nominal concentration of ciliates was either 0 or 12 ml^{-1} , and diatoms were added to the ciliate suspension at 6 different concentrations (60, 125, 250, 500, 1000 and 2000 *Thalassiosira weissflogii* ml^{-1}) yielding 12 different combinations, all incubated simultaneously. In another experiment the same amounts of diatoms were added to suspensions of 0.5 ciliates ml^{-1} . All other incubation experiments were designed to examine prey switching and the effect of turbulence on prey switching. Ideally, prey switching should be tested with constant total availability of prey, with the relative contributions of the 2 prey varying. However, availability is not easily defined or measured. The experiments were, therefore, designed as a

matrix with concentrations of both prey varying. Each experiment was conducted at a set concentration of diatoms and ciliates and incubations in still and turbulent chambers were done simultaneously. Altogether we conducted 14 experiments. Concentrations of diatoms and ciliates were varied from 60 to 2000 cells ml^{-1} and 1 to 25 cells ml^{-1} , respectively.

Behavioural observations. The behaviour of the copepods was investigated by filming *Acartia tonsa* adult females feeding in different combinations of diatoms and ciliates in 605 ml plexiglass aquaria (height 20 cm, width 5.5×5.5 cm). The filming equipment consisted of a CCD video camera (Mintron MTV 1802CD) equipped with a 105 mm macro lens (Vivitar Series 1), a super-VHS video cassette recorder (Panasonic NV-FS200 HQ), a time-code generator (Panasonic WJ-810), a video monitor and a light source. In the first experiments (Expts 1 and 2) a white light source filtered through a red filter (Ilford Safelight 906, 620 nm cut-off) was used; this provides about $3 \mu\text{E m}^{-2} \text{ s}^{-1}$. In the last experiment (Expt 3) infrared light was used. After acclimation to the experimental conditions the copepods did not seem to be disturbed by either of the light types.

The copepods were kept in filtered seawater overnight and then acclimated to the experimental conditions for at least 1 h prior to filming. Between 15 and 20 copepods were introduced into aquaria containing the different combinations of diatoms and ciliates (Table 1). Expt 2 and a bottle incubation experiment were conducted simultaneously with identical concentrations of diatoms and ciliates. Filming took place in a dark room at ca 20°C . Each aquarium was filmed for at least 20 min (up to 50 min), during which several different individuals were filmed. The camera lens was placed at 5 to 10 cm distance from the aquarium wall, and one animal at a time was kept in the focus of the lens through the turning of the camera on a tripod and manual focusing of the lens. The depth and width of the viewfield varied according to the dis-

Table 1. Concentrations of ciliates (*Strombidium sulcatum*) and diatoms (*Thalassiosira weissflogii*) used during behavioural observations of *Acartia tonsa*

| | Concentration | Aquaria filmed | Comment |
|-----------------------|-----------------------------|----------------|--|
| Expt 1 | | 4 | |
| <i>S. sulcatum</i> | 25 ml^{-1} | | |
| <i>T. weissflogii</i> | 60 to 2000 ml^{-1} | | |
| Expt 2 | | 6 | Filmed twice |
| <i>S. sulcatum</i> | 0 or 12 ml^{-1} | | Conducted simultaneously with bottle incubation experiment |
| <i>T. weissflogii</i> | 125 to 500 ml^{-1} | | |
| Expt 3 | | 12 | Experiment split in 2, each with 6 aquaria |
| <i>S. sulcatum</i> | 1 to 25 ml^{-1} | | |
| <i>T. weissflogii</i> | 0 or 250 ml^{-1} | | |

tance of the copepod from the camera and according to lens aperture size.

The video tapes were analyzed with a computer-based event recorder by logging the frequency of feeding bouts and sinking events (Saiz 1994), which are indicative of suspension feeding and ambush feeding, respectively. Different keyboard keys were assigned for these 2 mutually exclusive behaviours. Suspension feeding bouts were events in which a feeding current propelled the animal forward in a gliding movement; sinking events were periods between the suspension feeding bouts. Periods when the copepods were close to the surface, bottom or walls of the aquarium were excluded from the analysis. The duration of each of 50 to 100 feeding bouts was measured for each food condition by frame-by-frame analysis (resolution 0.02 s). The fraction of time spent in feeding bouts ('feeding bout activity') was calculated by multiplying the average feeding bout duration (from the frame-by-frame analysis) with the feeding bout frequency (from the real time analysis). The 'sinking activity' was then estimated as $(1 - \text{feeding bout activity})$, and the average duration of sinking events as $(\text{sinking activity}/\text{frequency of sinking events})$.

RESULTS

Functional response of *Acartia tonsa*

Acartia tonsa shows a sigmoid functional response (Holling type III) in diatom ingestion rate to variations in the concentration of *Thalassiosira weissflogii*: ingestion rate saturates at concentrations exceeding 500 cells ml^{-1} , while the clearance rate peaks at ca 250 cells ml^{-1} and declines at both higher and lower concentrations (Fig. 1). This pattern confirms earlier observations (Paffenhöfer & Stearns 1988). In the presence of alternative prey (ciliates) at a relatively high concentration (12 ml^{-1}) *A. tonsa* has the same principal type of functional response, but diatom feeding becomes depressed, particularly at the lower concentrations (Fig. 1). At a low concentration of alternative prey (0.5 ciliates ml^{-1}) the functional response is not significantly affected (data not shown). We did not conduct experiments explicitly designed to examine the effect of diatoms on the functional response of ingestion of ciliates by *A. tonsa*. However, data compiled from all experiments suggest that, in the presence of diatoms, ingestion of ciliates was unsaturated throughout the range of concentrations offered, and the clearance rate was independent of the concentration of ciliates (Fig. 2).

In the elucidation of behavioural mechanisms behind prey selection and switching, the dependency of

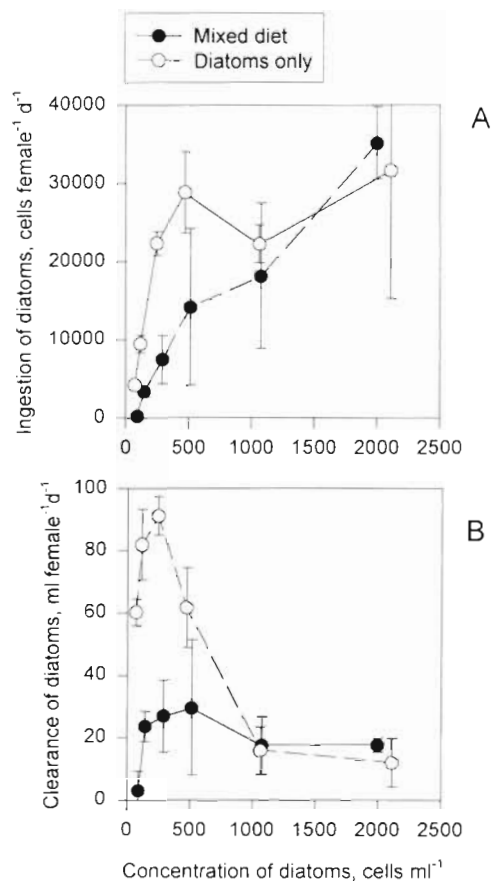


Fig. 1. *Acartia tonsa*. Calm water functional response to variations in the concentration of diatoms: (A) ingestion and (B) clearance. (O) Diatoms *Thalassiosira weissflogii* only; (●) *T. weissflogii* and ciliate *Strombidium sulcatum* added at a concentration of 12 ml^{-1} . Error bars show \pm SD

diatom clearance on diatom concentration (Fig. 1B) complicates matters. In the following, therefore, we primarily utilize data for which feeding is unsaturated and clearance is relatively independent of prey concentration; i.e. experiments with concentrations of diatoms between 125 and 500 ml^{-1} and concentrations of ciliates $< 20 \text{ ml}^{-1}$.

Prey selection and alternating feeding behaviours

We first hypothesized that feeding on diatoms prevents feeding on ciliates (and vice versa) because the more time spent feeding on diatoms (suspension feeding) the less time available for feeding on ciliates (ambush feeding). This hypothesis implies that the clearance rate on ciliates (F_{Cil}) is negatively correlated with the clearance rate on diatoms (F_{Diat}) at unsaturating concentrations (concentration of diatoms, C_{Diat} , less than 500 ml^{-1}). Since, however, there was no (negative

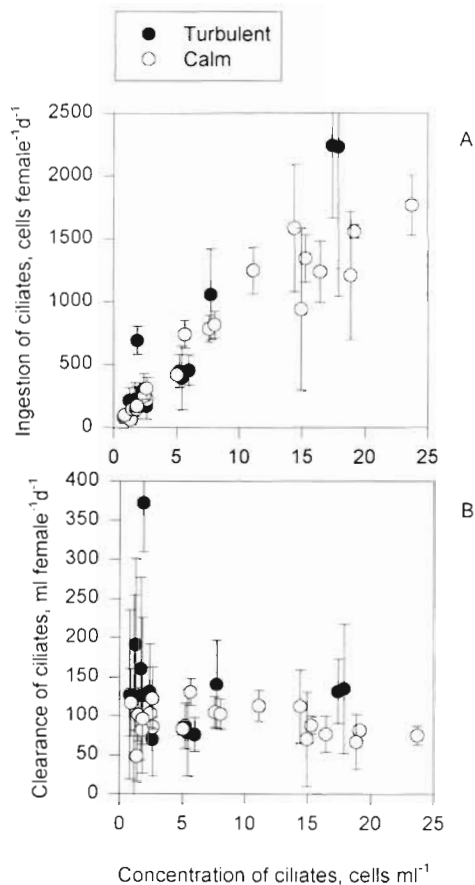


Fig. 2. *Acartia tonsa*. Functional response to variations in the concentration of ciliates: (A) ingestion and (B) clearance. Diatom *Thalassiosira weissflogii* added (60 to 2000 cells ml⁻¹) in all treatments. (O) Calm water; (●) turbulent water. Error bars show \pm SD

or otherwise) relation between F_{Dia} and F_{Cil} , our results do not support this hypothesis, either in calm or in turbulent water (Fig. 3)

Behavioural observations may help further explore this hypothesis, which implies that the fraction of time allocated to different behaviours would vary with the relative availability of the 2 prey. First, a comparison between swimming activity and simultaneously measured clearance rates on diatoms (Fig. 4) establishes the connection between bottle experiments and behavioural observations. F_{Dia} increased proportionally with swimming activity, thus supporting the assumption that feeding bouts are directly related to suspension feeding. Second, Fig. 5A demonstrates that feeding bout activity (i.e. suspension feeding) was higher (and sinking activity lower) in mixed suspensions of diatoms and ciliates than in pure suspensions of ciliates. It further shows that, in the mixed diet, sinking activity (i.e. ambush feeding) increased with increasing availability of ciliates, and eventually (at

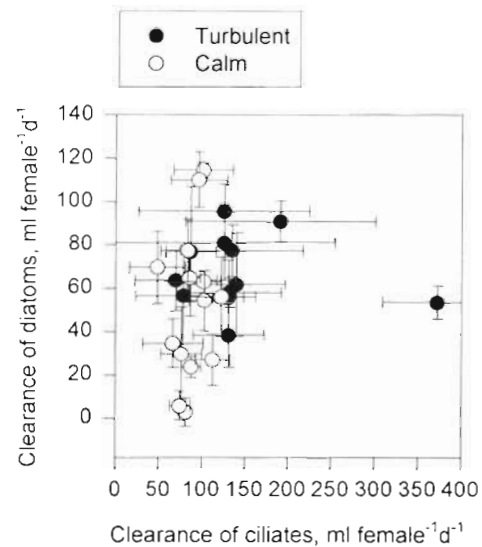


Fig. 3. *Acartia tonsa*. Relationship between clearance of diatoms and clearance of ciliates in mixed prey assemblages at non-saturating concentrations. (O) Calm water; (●) turbulent water. Error bars show \pm SD

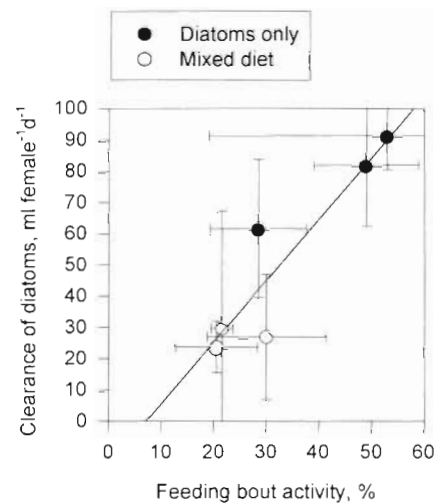


Fig. 4. *Acartia tonsa*. Clearance rate of diatoms by *A. tonsa* as a function of feeding bout activity: (O) mixture of diatom *Thalassiosira weissflogii* and ciliate *Strombidium sulcatum*; (●) *T. weissflogii* only. Feeding bout activity and clearance were measured in separate experiments conducted simultaneously. The regression is statistically significant ($n = 6$, $r^2 = 0.84$, $p < 5\%$). Error bars show \pm SD

25 ciliates ml⁻¹) reached the level attained in a pure ciliate suspension (i.e. almost 100% sinking activity). Thus, there was a progressive change in feeding behaviour, as predicted. We note that this is an apparent contradiction of the results in Fig. 3.

The average duration of both sinking and suspension feeding events also varied with the composition of

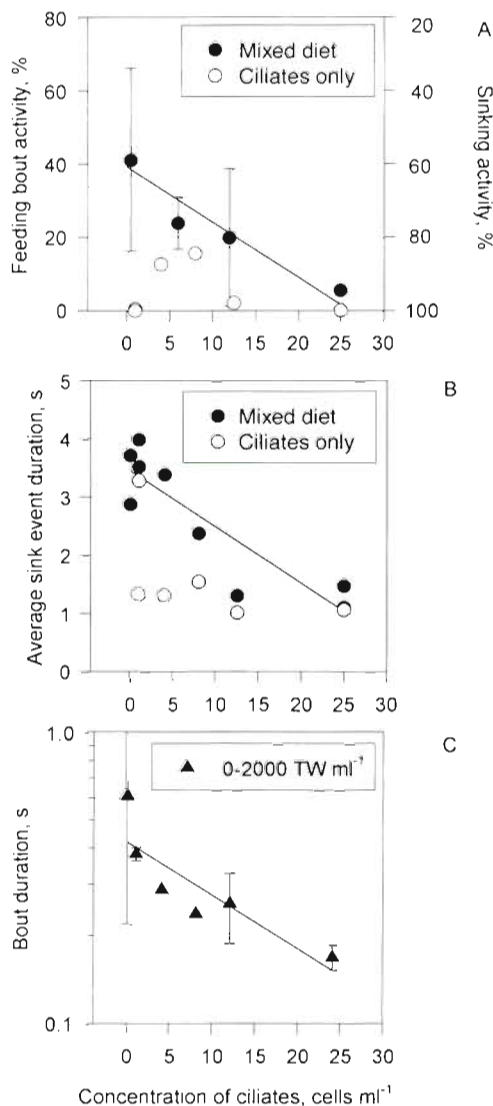


Fig. 5. *Acartia tonsa*. (A) Feeding bout activity and sinking activity as a function of the concentration of ciliates: (O) ciliate *Strombidium sulcatum* (●) mixture of diatom *Thalassiosira weissflogii* (250 cells ml⁻¹) and *S. sulcatum*. The regression for mixed suspensions is statistically significant ($n = 11$, $r^2 = 0.41$, $p < 5\%$). (B) Average sink event duration as a function of the concentration of ciliates: symbols as in (A). The regression for mixed suspensions is statistically significant ($n = 9$, $r^2 = 0.79$, $p < 5\%$). (C) Average feeding bout duration as a function of the concentration of ciliates: (▲) mixture of diatom *T. weissflogii* (0 to 2000 cells ml⁻¹) and *S. sulcatum*. The regression is statistically significant ($n = 22$, $r^2 = 0.52$, $p < 5\%$). Error bars show \pm SD

available food in a consistent way (Fig. 5B, C). In pure suspensions of ciliates, the duration of sinking events consistently (except for 1 observation) averaged about 1 s, while in mixtures they were significantly longer. With increasing (relative) concentration of ciliates, the duration of sinking events declined to that realised in a

pure suspension of ciliates. Feeding bout duration was independent of the concentration of diatoms, but it declined significantly with the concentration of ciliates (stepwise multiple regression). The exact significance of these patterns is unclear, but they do demonstrate that there is a distinct behavioural response to food composition.

Prey switching

We next hypothesized that *Acartia tonsa* feeds mostly on the prey item from which it gets the highest gain per unit time. This implies that *A. tonsa* switches from one prey species to the other as the relative concentrations of prey change. The null hypothesis is that the ratio of clearance rates of the 2 alternative prey ($F_{Cil}:F_{Dia}$) is constant and independent of the relative availabilities of the 2 prey. Fig. 6 demonstrates that the ratio $F_{Cil}:F_{Dia}$ did increase significantly with increasing relative availability of ciliates, at least in calm water, and the null hypothesis must therefore be rejected; i.e. there was switching.

The experimental design allows one to look further into the components of this switching and to examine whether the clearance rate (i.e. time spent feeding) on one prey changes as a function of the concentration of the other. The switching hypothesis can then be recast as: clearance of one prey decreases with increasing concentration of the other.

The calm-water rate of diatom clearance declined significantly with increasing ciliate concentration

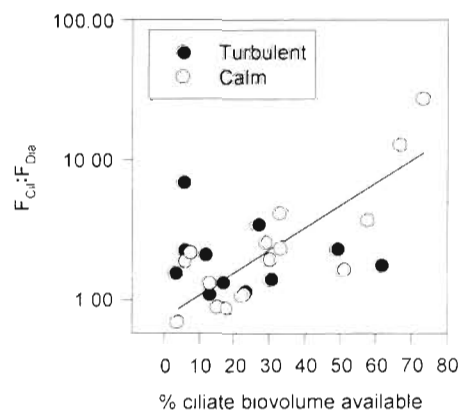


Fig. 6. *Acartia tonsa*. Ratio of clearance rates of ciliate *Strombidium sulcatum* to diatoms *Thalassiosira weissflogii* ($F_{Cil}:F_{Dia}$) as a function of the relative availability of ciliates in the diet (as biovolume) in calm (O) and turbulent (●) conditions. Only experiments with concentrations of diatoms between 125 and 500 ml⁻¹ are included. The regression for calm conditions is statistically significant ($n = 15$, $r^2 = 0.67$, $p < 5\%$).

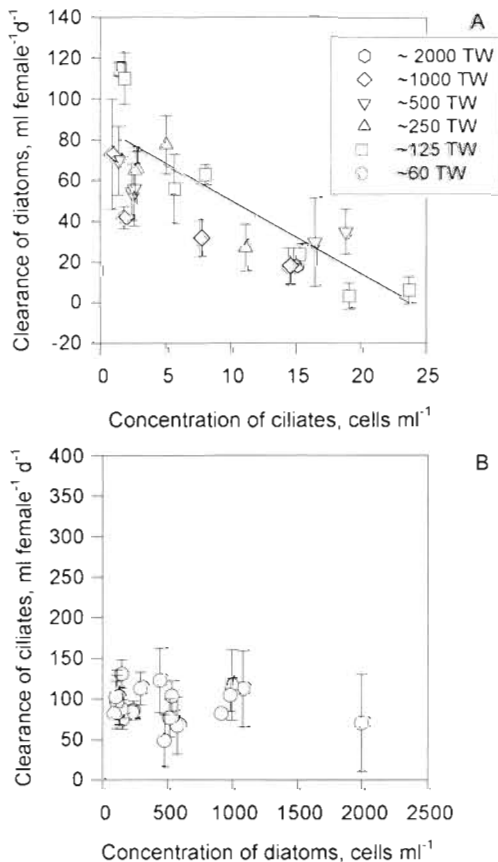


Fig. 7. *Acartia tonsa*. Calm water clearance rate in mixed prey assemblages. (A) Clearance of diatom *Thalassiosira weissflogii* (TW) as a function of the concentration of ciliate *Strombidium sulcatum*. The different nominal concentrations of diatoms ml⁻¹ used have been distinguished. The regression is $F_{Diat} = 85.4 - 3.6 C_{Cil}$ ($n = 15$, $r^2 = 0.71$, $p < 5\%$) and includes only observations where the concentration of diatoms is between 125 and 500 cells ml⁻¹. (B) Clearance of ciliates as a function of the concentration of diatoms. Error bars show \pm SD

(Fig. 7A). Thus, clearance of diatoms does depend on the concentration of ciliates. The calm water clearance rate on ciliates, on the other hand, was almost constant and independent of the concentration of diatoms (Fig. 7B). It averages 93 ± 21 ml ind.⁻¹ d⁻¹.

Effect of turbulence on prey selection

Our final hypothesis was that turbulence changes prey selection towards ciliates. This hypothesis implies (1) that a plot of F_{Diat} versus C_{Cil} yields a lower intercept and a smaller slope in turbulent than in calm water and (2) that a plot of F_{Cil} versus C_{Diat} yields a higher intercept and a steeper slope in turbulent than in calm water. The plot of diatom clearance versus ciliate con-

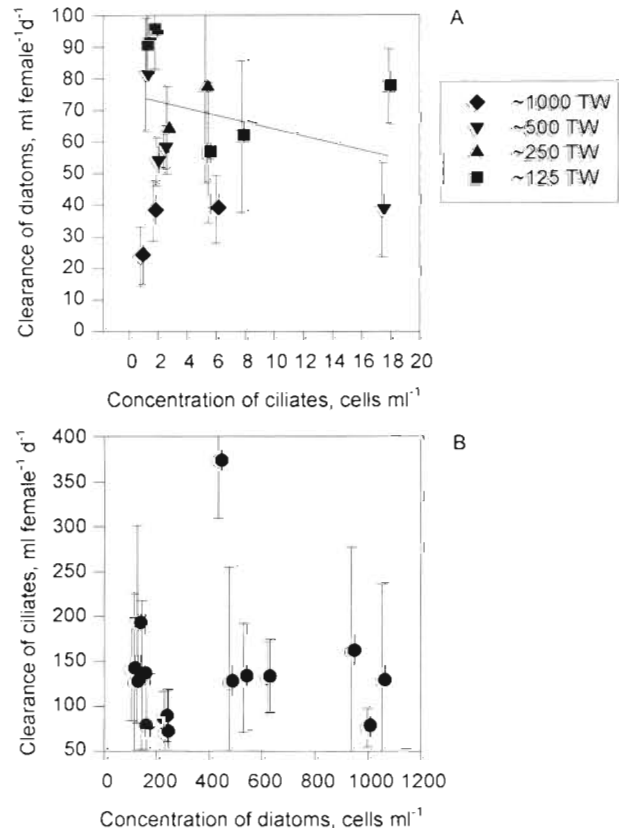


Fig. 8. *Acartia tonsa*. Turbulent water clearance rate in mixed prey assemblages. (A) Clearance of diatom *Thalassiosira weissflogii* (TW) as a function of the concentration of ciliate *Strombidium sulcatum*. The different nominal concentrations of diatoms ml⁻¹ used have been distinguished. The regression is $F_{Diat} = 75.0 - 1.1 C_{Cil}$ ($n = 11$, $r^2 = 0.15$, $p > 5\%$) and includes only observations where the concentration of diatoms is between 125 and 500 cells ml⁻¹. (B) Clearance of ciliates as a function of the concentration of diatoms. Error bars show \pm SD

centration in turbulent conditions (Fig. 8A) compared to that for calm water (Fig. 7A) supports this hypothesis. The 2 regressions (including only data for 125 to 500 *Thalassiosira weissflogii* ml⁻¹) do differ significantly since the slope is smaller ($p < 5\%$) and the intercept lower (not significant) in turbulent compared to calm water. In contrast, the (lacking) relationship between ciliate clearance and diatom concentration in turbulent water provides no evidence for the hypothesis (Fig. 8B): clearance rate on ciliates was independent of diatom concentration in turbulent water. It averaged 139 ± 75 ml ind.⁻¹ d⁻¹.

The hypothesis also implies that the ciliate-to-diatom clearance rate ratio is higher in turbulent than in calm water. In Fig. 9 the ratio in turbulent water has been plotted against the ratio in calm water. The majority of the observations fall above the 1:1 line, and the ratio is on average significantly higher in turbulent than in calm water (signed rank test, $p < 5\%$).

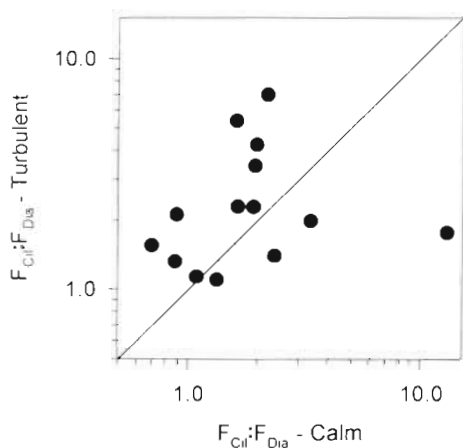


Fig. 9. *Acartia tonsa*. Ratio of clearance rates of ciliates to diatoms ($F_{Cil}:F_{Dia}$) in turbulent versus calm water. Line is $x = y$

DISCUSSION

Encounter tactics, prey selection, and prey switching

Our data demonstrate that prey switching occurs in *Acartia tonsa*, and that it is caused mainly by a change in clearing of diatoms with changing prey composition. Our data also document that turbulence changes prey selection towards motile prey (ciliates), although the effect was less than expected. Finally, our observations clearly demonstrate a change in feeding behaviour with a change in the relative concentrations of the 2 alternative preys, which is consistent with switching. However, the different sets of observations are not immediately compatible.

Based on the behavioural observations of Jonsson & Tiselius (1990) we hypothesized that selection between motile and non-motile prey in *Acartia tonsa* is based on different encounter tactics. Our data are consistent with the idea that diatoms are encountered and captured only by *A. tonsa* in the suspension feeding mode. The evidence is (1) feeding bout activity (fraction of time in suspension feeding mode) is closely related to the clearing of diatoms (Fig. 5), (2) feeding bout activity is higher in the presence of diatoms than in a pure suspension of ciliates, and in mixtures it declines with increasing relative concentration of ciliates, as does the clearing of diatoms (Figs. 4 & 7A), and (3) the effect of turbulence on the clearance of diatoms is negligible, as predicted for the suspension feeding mode (Kjørboe & Saiz 1995). This is further supported by the finding of Jonsson & Tiselius (1990) that the fraction of time *A. tonsa* moves its feeding appendages (suspension feeding) increases with increasing concentrations of phytoplankton in the presence of ciliates.

The observed change in behaviour with a change in the relative concentration of ciliates is also consistent with the idea that ciliates are encountered and captured in the ambush feeding mode. First, time allocated to sinking (i.e. ambush feeding) increases with increasing relative availability of ciliates. Second, sink event duration in a pure suspension of ciliates is about 1 s, as found previously (Jonsson & Tiselius 1990), and in mixtures of the 2 prey this duration is approached as the relative concentration of ciliates increases (Fig. 4B). Together, these observations suggest that *Acartia tonsa* changes to almost 100% ambush feeding as the relative concentration of ciliates increases, as was predicted. However, the clearance of ciliates did not change as expected from the variations in the time budget. In fact clearance of ciliates was constant and independent of the relative concentrations of the 2 prey. This does not mean that the presence of diatoms has no effect on *A. tonsa* clearance of ciliates, as becomes clear when the present data are compared with those of Saiz & Kjørboe (1995). That study comprised single-prey experiments conducted in the same laboratory as the present experiments, with identical techniques and identical cultures and clones of predator and prey. The comparison shows that (1) in the absence of diatoms *A. tonsa* clears ciliates at a rate twice that in the presence of diatoms (182 ± 8 and 93 ± 21 ml female⁻¹ d⁻¹, respectively, $p < 5\%$), (2) the effect of turbulence on the clearing of ciliates is substantial in the absence of diatoms (increases by a factor of ca 4 to ca 700 ml female⁻¹ d⁻¹) but modest in the presence of diatoms (increase at most by 50%), and (3) in the absence of diatoms the ingestion of ciliates saturates at a concentration of <20 ml⁻¹, while in the presence of diatoms it continues to increase up to ± 20 ciliates ml⁻¹ (Fig. 2).

These apparently contradictory observations can be reconciled if we assume that ciliates can be encountered and captured both in the ambush and in the suspension feeding modes. At low relative concentrations of ciliates, copepods mainly suspension feed; this would explain why ciliates and diatoms are cleared at similar rates, and why there is no strong effect of turbulence. At higher relative concentrations of ciliates, ambush feeding dominates and ciliate feeding becomes saturated. At a concentration of 20 ciliates ml⁻¹, for example, where *Acartia tonsa* almost exclusively ambush feeds (see Fig. 4), a clearance rate of ca 100 ml female⁻¹ d⁻¹ is predicted on the basis of experiments conducted with only this prey (Saiz & Kjørboe 1995); this predicted rate is close to that actually observed here. At near saturating concentrations of ciliates, the effect of turbulence on ciliate feeding vanishes (Saiz & Kjørboe 1995); again, this is consistent with the present observations. Finally, the weaker than expected

change in selection in turbulent conditions is also consistent with this idea.

The ability of *A. tonsa* to capture the ciliate *Strombidium sulcatum* in its feeding current—or the inability of *S. sulcatum* to escape the feeding current—is probably specific to this particular ciliate. *S. sulcatum* may not be a good representative of planktonic ciliates, since it is semi-benthic (Fenchel & Jonsson 1988). Other ciliates, such as the widespread *Mesodinium rubrum*, have a demonstrated escape capability that considerably exceeds that of *S. sulcatum* (Jonsson & Tiselius 1990), and might be more representative of microzooplankters. Copepod nauplii and other microzooplankters have also been shown to perceive and escape predators efficiently (e.g. Williamson & Vanderploeg 1988, Buskey 1994). We suggest that capture of such prey would be negligible by *A. tonsa* in the suspension feeding mode and that microzooplankton predation would decrease in the presence of abundant phytoplankton. This has actually been observed in *A. tonsa* feeding in mixtures of phytoplankton and various planktonic ciliates (Stoecker & Egloff 1987).

Prey selection in *Acartia tonsa* has here and in Jonsson & Tiselius (1990) been given a mechanistic interpretation. Previous observations of alternate feeding of *A. tonsa* on motile (ciliates, nauplii) and non-motile (phytoplankton) prey have shown quite variable results, which may now be reinterpreted in light of the present findings. For example, Lonsdale et al. (1979) found that the feeding rates on both phytoplankton and motile prey were independent of the presence of alternative prey, while Anraku & Omori (1963) found that feeding on both types of prey were reduced in the presence of alternative prey, and both Stoecker & Sanders (1985) and Stoecker & Egloff (1987) observed that feeding on motile prey was most often reduced in the presence of phytoplankton. These observations may all be accommodated by the present demonstration of flexible encounter tactics, which depend on the relative availability of alternative prey, and by noting that the ability of *A. tonsa* to capture motile prey in the suspension feeding mode will depend on the characteristics of the particular prey.

Prey switching has previously been demonstrated in a few aquatic invertebrates (Murdoch 1969, Lawton et al. 1974, Butler & Burns 1991), and several authors have examined prey switching in copepods. However, most authors have been unable to demonstrate prey switching in copepods (Lonsdale et al. 1979, Mullin 1979, Greene & Landry 1985), and Stoecker & Sanders (1985) claimed that *Acartia tonsa* did not show switching between ciliate and phytoplankton prey, even though their data clearly demonstrates switching (their Fig. 7). The previous most convincing demonstration of prey switching in a copepod was provided by Landry

(1981), who showed that *Calanus finmarchicus* fed disproportionately on the most abundant (in terms of biomass) of 2 prey (a phytoplankter and copepod nauplii). Prey switching does not imply a particular mechanism, and several mechanisms can produce switching. For example, a type III functional response with reduced feeding effort (clearance) at low prey concentrations may produce switching. The present study is the first demonstration of prey switching in a copepod caused by a change in behaviour. *C. finmarchicus* does have a type III functional response, and Landry (1981) was unable to decide whether prey switching in this species was due to a response to the relative composition of the prey or to the absolute concentrations of individual prey organisms. However, given the similarities between *A. tonsa* and *C. finmarchicus* in the use of different feeding modes for diatoms (suspension feeding) and microzooplankton (active mechanoreception) (Landry 1980), it is likely that prey switching in *C. finmarchicus*, like that in *A. tonsa*, is caused by a change in the time allocated to different feeding behaviours as a function of the relative availability of the 2 prey organisms. Because the 2 different feeding modes described for *A. tonsa* apply to a number of other neritic copepods (Tiselius & Jonsson 1990), it is likely that prey switching is widespread among them. This is corroborated by evidence from field studies of prey switching in several species of copepods (e.g. Gifford & Dagg 1988, Kleppel et al. 1988, Fessenden & Cowles 1994).

Implications

Prey switching has been implicated as a potential population stabilizing mechanism (Oaten & Murdoch 1975), also in planktonic food webs (e.g. Landry 1981), because it provides refuge for rare prey, thereby preventing their extinction. This potentially stabilizing effect, however, is already implicit in the type III functional response, which has now been convincingly demonstrated for several copepods (e.g. Landry 1981, Kjørboe et al. 1985, Paffenhöfer & Stearns 1988; see also Fig. 1), and we shall not discuss it further here. Prey switching may have other implications for pelagic food web structure. For example, Nielsen & Kjørboe (1994) noted that seasonal peaks in the abundance of oligotrich ciliates in the Kattegat co-occurred with peaks in phytoplankton biomass, even though the ciliates were growing at maximal rates throughout the year and were, thus, not food limited. They explained this as a result of relaxed copepod predation on ciliates during periods of high phytoplankton abundance and, thus, by assuming prey switching. Because copepods are frequently the main source of mortality for micro-

zooplankton and are capable of controlling microzooplankton populations (Smetacek 1981, Stoecker & Sanders 1985, Dolan 1991, Kivi et al. 1993, Nielsen & Kjørboe 1994), prey switching may provide survival windows to ciliates and other microzooplankton during blooms of phytoplankton. This may explain why microzooplankton populations often peak concurrently with net phytoplankton blooms, and apparently independently of their own food (e.g. Smetacek 1981, Hansen 1991, Kivi et al. 1993, Nielsen et al. 1993).

Switching also has implications for the predator. Prey switching normally secures the most efficient feeding in terms of the amount of food being eaten per unit time. However, switching may imply a decrease in the diversity of the diet because the predator tends to feed mainly on the most abundant prey. Kleppel (1993) argued that copepods depend on eating a nutritionally complete and, therefore, varied diet, and prey switching might therefore appear an inadequate strategy. However, because the biomass of ciliates and other motile prey is typically less than that of the phytoplankton in the eutrophic environments encountered by *Acartia tonsa* and other neritic copepods, continued suspension feeding would lead to a herbivorous diet. Flexible encounter tactics and prey switching allow *A. tonsa* to include animal prey in the diet during periods of high microzooplankton abundance, and this strategy, therefore, appears adaptive in fluctuating neritic environments.

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